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## Burrowing behavior of the midwife toads *Alytes cisternasii* and *Alytes obstetricans* (Anura, Discoglossidae)

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The European midwife toads *Alytes cisternasii* and *Alytes obstetricans* are fossorial anurans that primarily use their forelimbs in burrowing. The maneuverings are quite dexterous and the forelimbs are used alternately or sometimes synchronously. The fingers (particularly III and IV) are oriented downward and scraped into the substrate. Occasionally the head is pushed into the substrate or acts in a scoop-like manner. The toads construct a system of tunnels and cavities underground. They do push-ups packing the substrate against the top of the tunnel with their head. The toads also vocalize and form aggregations (2-5 individuals) underground suggesting social interactions. The two species are quite similar in motor patterns of forward burrowing. However, *A. cisternasii* makes minimal use of its hind limbs (only for bracing), whereas *A. obstetricans* actively uses its hind limbs to kick soil posteriorly that was brought to the surface by the forelimbs. Also, *A. cisternasii* is a rapid, efficient forward burrower that is highly fossorial, whereas *A. obstetricans* is a reluctant forward burrower that lingers on the surface and prefers pre-existing holes. Differences in burrowing behavior of the two species are correlated with differences in morphology and habitats occupied. In four instances in which the burrowing of male *A. obstetricans* carrying eggs was studied, no differences were observed in motor patterns from other adults not carrying eggs. Kicking of the hind legs was carried out in a manner that assured the egg masses were not damaged. It is probable that the main reason forward burrowing evolved in *Alytes* was to assure subsurface concealment because of the involvement of the male's hind limbs in parental care.



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## INTRODUCTION

Over the past 40 years a vast amount of information has been gathered on the reproductive biology of anurans. Most of these data were obtained during the breeding season which represents only a small (although extremely important) portion of the life cycle. Little is known about the ecology and behavior of many species during other periods of the life cycle when the animals tend to be more secretive. This is particularly true for the many fossorial species that disappear from view and are thus extremely difficult to study.

The fossorial behavior and ecology of the chorus frogs *Pseudacris ornata* (Holbrook, 1836) and *Pseudacris streckeri illinoensis* Smith, 1951 of North America were investigated by BROWN et al. (1972), AXTELL & HASKELL (1977), BROWN (1978), BROWN & MEANS (1984), BROWN & ROSE (1988), TUCKER et al. (1995) and BROWN & CIMA (1998). These species are highly unusual in that they use their forelimbs in forward burrowing, whereas the vast majority of other fossorial anurans burrow backwards with their hind limbs.

Two other species known to burrow with their forelimbs are the midwife toads *Alytes cisternasii* Boscá, 1879 (fig. 1) from the Iberian Peninsula and *Alytes obstetricans* (Laurenti, 1768) (fig. 2) of western Europe (BOULENGER, 1896; SCHREIBER, 1912; HELLMICH, 1962; ARNOLD & BURTON, 1978). Although there has been considerable research on the courtship and reproduction of these toads, particularly in the last 15 years, little is known about their burrowing behavior. The morphological adaptations of the forelimb and anterior portion of the body for burrowing (CRESPO, 1979, 1982a-b; SANCHIZ, 1984; BRITO-E-ABREU et al., 1996), preliminary behavioral observations (CRESPO, 1981) and the well-known male parental care in which the eggs are wrapped around the hind legs (BOULENGER, 1896; SCHREIBER, 1912; DE WITTE, 1948; MARQUEZ & VERRELL, 1991; NÖLLERT & NÖLLERT, 1992) suggest that the method(s) of burrowing would be of considerable interest. Thus, the objective of this study was to carry out a detailed investigation of the burrowing behavior of *A. cisternasii* and *A. obstetricans*.

## MATERIALS AND METHODS

Ten *A. cisternasii* and eight *A. obstetricans* were collected from Portalegre (Province of Alto Alentejo, Portugal) and Gerês (Province of Minho, Portugal), respectively, under a collection permit given by Serviço Nacional de Parques Reservas e Conservação da Natureza (currently Instituto de Conservação da Natureza) to EGC. These specimens were sent by air to Illinois State University, Normal, Illinois, USA. All animals arrived alive and in good health.

Each species was housed separately in 75.7 liter aquaria (61.5 cm long, 31.5 cm wide, 41.5 cm high). The aquaria were filled to a depth of 15 cm with sand of the Plainfield-Bloomfield Association (CALSYN, 1995) from an undisturbed area of Sand Ridge State Forest in northern Mason County, Illinois. Water was periodically sprinkled on the sand to keep it slightly moist. A finger bowl (5.5 cm high, 12.0 cm diameter) partially filled with water (changed daily) was placed on the surface of the sand in each aquarium. Ambient temperature was a constant

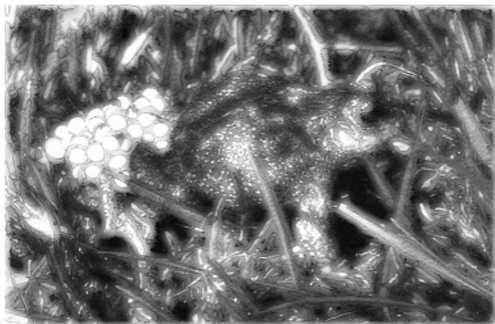


Fig. 1. - Male tree frog *Allysia robusta* carrying egg (Doolittle, Province of Aho, Ahangé, Suruga, 1997).

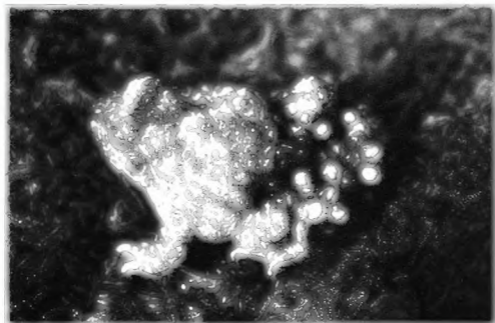


Fig. 2. - Male tree frog *Allysia ducurana* carrying egg (Datta, Province of Malabar, Kerala, 1983).

25°C. The photoperiod was 8.5 h light/15.5 h dark. Illumination was provided by white fluorescent ceiling lights. Mealworms were fed ad libitum in the lower half of a petri plate. Feces and any dead mealworms were removed when evident.

Behavioral observations were made on 64 dates over a 169-day period (25 April through 10 October). Durations of observations ranged from a few minutes for incidental observations to 5-6 hours for structured observations. Sometimes two or more sessions were carried out during a given 24 h period. Observations were made under six different conditions. First, incidental observations were made on *Alytes* in their holding aquaria (both on the surface and when buried underneath sand, as viewed through the glass). Second, for formal observations, specimens were individually placed in an aquarium of the same dimensions and sand depth as the holding aquaria. Brown paper was taped on three sides of this aquarium, and a V-shaped viewing hood was attached to the fourth (long) side. It soon became evident (from the heretofore mentioned incidental observations) that the *Alytes* seemed unaffected by the human observer. Thus, the hood was removed to facilitate observer visibility. The sand surface was leveled before each animal was tested. Burrowing was timed with a stopwatch. After initial observations were completed, a flat rock was placed on the sand surface to observe the reactions of each *Alytes*. A small red light mounted 1 m over the aquarium facilitated nocturnal observations. Third, a video camera was mounted above each of the aforementioned aquaria. The camera was wired to a monitor in a distant location of the laboratory for remote viewing. Fourth, subterranean burrowing was observed in the giant "ant farm" apparatus utilized by BROWN & MEANS (1984) to study *P. ornata*. This chamber has a plate glass front and stainless steel plate back. The chamber is 91.2 cm long and 57.5 cm high. Grooves in the side boards supporting the steel plate back allow the depth of the chamber to be adjusted according to the width of the anuran. A plywood hood around the front of the chamber partially shades the viewing area and prevents disturbance of burrowing frogs. The chamber was filled with slightly moistened sand and *Alytes* were placed on the surface. Fifth, burrowing was viewed ventrally through the glass bottom of a smaller aquarium (36.0 cm long, 21.5 cm wide, 26.0 cm high) with only 2.5 cm of sand on the bottom. The ends of the aquarium were mounted on pedestals and LEB laid on his back on the lab table with his head underneath the aquarium. A small microscope lamp aided the observation of the *Alytes* as they moved their forehands against the glass aquarium bottom. An assistant observed the *Alytes* on the surface and alerted LEB as to direction and progress in burrowing. Sixth, juvenile *A. obstetricans* were studied during metamorphosis. Adult males carried eggs four times (one was a double clutch from more than one female) during this study. After a period of care, the eggs were released by the males in the finger bowl in the aquarium. Eggs and newly hatched tadpoles were transferred to other aquaria for rearing. Tadpoles were fed Tetramin. Water level was maintained at a depth of ca. 5 cm. With the approach of metamorphosis, one end of the aquarium was elevated and sand was placed above the water line.

Nocturnal surface emergence was determined by: (1) direct observation; (2) disturbance of the sand surface (which was leveled every day by LEB); (3) deposition of sand into the finger bowl and petri plate (which were cleaned every day); (4) consumption of mealworms; (5) presence of feces on the surface.

## RESULTS

*ALYTES CISTERNASII**Preburrowing patterns*

When *A. cisternasii* were placed on the surface of the sand they sometimes initiated burrowing immediately. More commonly they first crawled a short distance and/or took one or a few hops. Often the toad lowered the anterior portion of the head at an angle to the sand surface and moved forward, plowing a short furrow (ca. 2-4 cm). From 1-3 furrows were plowed before initiation of burrowing. Presumably this functioned to test the friability of the substrate for selection of a suitable site for digging. Sometimes the head was lowered but no furrow was produced during forward movement.

*Burrowing behavior*

Burrowing was initiated by simultaneously lowering the anterior end of the head (if not already in that position from plowing) and rapidly digging a hole with the forelimbs. One to several strokes were made with one forelimb before changing to the other forelimb. Occasionally both forelimbs were used at the same time. The dexterous maneuverings of the forelimbs were anterior to posterior in direction and variably moved laterally or sometimes ventrally in an arc-like manner. The head was often pushed into the sand and thus complemented the action of the forelimbs. Sometimes the head scooped away sand. The eyes were partially withdrawn into the orbits during these maneuvers. There were frequent short pauses in digging during which the toad sometimes wiped sand off its eyes and peered up over the substrate. Rapid gular movements indicated heavy respiration. Mean time for burrowing (from initiation until entirely covered with sand) was 83.8 s (range: 38.3-166.7,  $n = 10$ ).

When viewed ventrally, the ends of the two outer fingers (III and IV) were oriented downward and scraped into the sand (and glass bottom of the aquarium). The tips of these fingers are heavily keratinized and darkened (CRESPO, 1982*b*; fig. 3). As the hand reached forward, the fingers were spread apart; as the hand moved backwards, the fingers were brought closer together and curled inwards. The first and second fingers did not make initial contact with the glass bottom of the aquarium. The keratinized palmar (metacarpal) tubercles (fig. 3) rarely touched the glass. When at rest, the hands were held against the sides or underneath the pectoral region.

The hind limbs were not used in digging. They were often passively folded in the same manner as when sitting, even when the posterior end of the body was tilted upward during forward burrowing. Sometimes one or both hind limbs were extended posteriorly for bracing. Occasionally they slipped from this position giving the impression that sand was being kicked posteriorly, but this did not seem to be an intentional movement by the toad.

When the rock was placed on the sand, the toads often oriented toward it and burrowed next to it. Under natural conditions, such a location might offer advantages such as protection from predators, more moisture, and possibly easier digging.

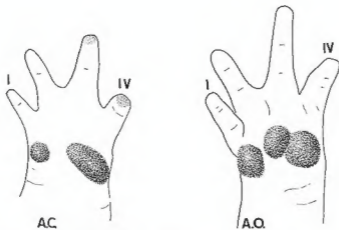


Fig. 3. – Ventral views of left hands of midwife toads. A. C., *Alytes cisternasii*; A. O., *Alytes obstetricans*. Stippling indicates keratinization. The large keratinized structures at the base of the hands are palmar (metacarpal) tubercles. Note keratinization at the ends of digits III and IV of *A. cisternasii*. Drawings modified from CRESPO (1982b).

The angle of burrowing was highly variable: from straight downward perpendicular to the surface, to nearly parallel to the surface, or at any angle in between. Furthermore, the toads often made abrupt changes in direction that differed markedly from the originally chosen course (particularly when they encountered the glass side of the aquarium). On some occasions, toads were even observed burrowing while upside down (venter oriented upward).

#### *Subterranean activities*

When burrowing was viewed in the “ant farm” apparatus, the patterns were much the same as when viewed on the surface: forelimbs alternately removed sand in front of the animal and the head was butted into the sand. Usually there was bracing with the hind limbs. Another behavior not heretofore seen on the surface was the use of the forelimbs to secondarily move sand along the sides of the body.

In the holding aquarium, the toads constructed a system of tunnels and cavities. Through the sides of the aquarium and in the “ant farm” apparatus, the toads were often seen doing push-ups, packing the sand against the top of the tunnel. When the toads were removed from underneath the sand, there was usually sand caked on top of the snout and/or head. The tunnels/cavities were stabilized somewhat by this behavior, although these structures were temporary because of the extensive subterranean movements of the toads.

When toads were removed from underneath the sand in the holding aquarium, they were often found in clusters of 2-3 individuals, suggesting attraction to one another and social interactions. The toads also diurnally vocalized underground (although infrequently) during the first month in the laboratory.

### Nocturnal activity

During diurnal hours, *A. cisternasii* remained buried under sand. However, toads were frequently directly observed on the surface at night. On other nights when observation was not undertaken, nocturnal surface activities of the toads were evident the following morning by: (1) new holes in the sand surface; (2) small new mounds of sand on the surface; (3) sand deposited in the water of the finger bowl; (4) sand deposited in the petri plate used to feed mealworms; (5) consumption of all or most of the mealworms; (6) feces on the sand surface. Besides feeding and hydration, surface activities included digging, defecating and exploration. Surface activity was considerably reduced after one month in the laboratory.

### ALYTES OBSTETRICANS

#### Preburrowing patterns

Prior to burrowing, *A. obstetricans* usually took a few hops and/or crawled forward. Only rarely was a furrow plowed with the head (which was typical behavior for *A. cisternasii*). Toads moved toward and into any pre-existing holes that were present in the surface (which was often the case in the holding aquarium).

#### Burrowing behavior

The motor patterns of the forelimbs and head of *A. obstetricans* were basically similar to those of *A. cisternasii*. However, the head was used to only a limited extent in surface burrowing by *A. obstetricans*. Furthermore, the hind limbs played a major role in assisting forward burrowing by kicking sand posteriorly after it was brought to the surface by the forelimbs. The animals were never observed to burrow backward (although SCHREIBER, 1912, indicated that the hind limbs are occasionally used for digging). *Alytes obstetricans* was also a slow burrower. There were long pauses between bouts of digging, and often a toad abandoned one site and moved to another location. Individuals often remained on the surface for an hour or more. Thus, timing the digging behavior was not feasible. Toads preferred to use existing holes, if available.

When viewed ventrally through the glass-bottomed aquarium, the fingers were used to scrape away sand, but progress was quite slow. When the rock was placed on the sand surface, the toads often moved toward it and started burrowing. However, they frequently stopped and relocated to another area.

#### Burrowing by males carrying eggs

Burrowing of four male *A. obstetricans* carrying eggs was studied. No differences were observed in motor patterns of these males and other adults not carrying eggs. The egg masses extended beyond the posterior edge of the hind limbs when the toads were at rest and the legs were folded in normal sitting position. When the males kicked sand with the hind limbs, the eggs were not dislodged because (1) the egg mass was attached in the distal one-half of the tibiofibula area, and (2) the plantar-digital area of the foot was used to kick sand. Males

kicked with one foot or both feet at the same time with no apparent disruption of the egg mass.

#### *Subterranean activities*

The motor patterns for subterranean digging were the same as those used on the surface. Push-ups were also utilized to aid in the construction of numerous tunnels and cavities. Thus, sand was often caked to the top of the head when animals were removed from underneath sand of their holding aquarium. The tunnels were mostly temporary.

*Alytes obstetricans* also constructed shallow holes. When the toads entered these cavities, they turned around and faced the opening. The anterior end of the head was positioned just behind the upper lip of the slanted cavity. Under natural circumstances, this position would still provide concealment, but would allow the animal to make a sudden exit to pursue passing prey or a potential mate.

Aggregations of 2-5 toads were encountered when animals were removed from the sand of the holding aquarium, implying mutual attraction or social interactions. Extensive subterranean vocalizations were produced during diurnal hours throughout most of the period of this study.

#### *Nocturnal activity*

*Alytes obstetricans* remained buried under sand during the day but exhibited nocturnal surface activity. This was evident by direct observation and indirectly by characteristics of the holding aquarium delineated for *A. cisternasii*. Surface behaviors included feeding, hydration, exploration, digging, defecating, frequent entering and exiting from pre-existing holes, vocalizing, courtship, and release of eggs into the finger bowl by parental males. Nocturnal activities were extensive and long-term, lasting throughout the study. The same activity cycles were followed by males carrying eggs: they remained buried during the day and emerged at night.

#### *Burrowing by juveniles*

Cavities were constructed by numerous metamorphosing juveniles. The forelimbs of these animals had protruded, the hind limbs were enlarged, and they still retained most of the tail. They were equivalent to developmental stages 42 and 43 of GOSNER (1960). The small cavities were dug in the sloping sand a short distance above the edge of the water. The juveniles sat in these cavities each with its head facing outwards toward the opening and with most of its body concealed. The tail was wrapped around the side of the body. Some juveniles sought cover under a nearby stone. Under natural conditions this behavior would provide juveniles with some protection from predators at this vulnerable stage in their life history.



## DISCUSSION

The two species of *Alytes* are similar in their motor patterns of forward burrowing, but they differ in two important ways. First, *A. cisternasi* makes minimal use of the hind limbs; they are either passively folded in the sitting position or used for bracing. In contrast, *A. obstetricans* actively uses the hind limbs to kick sand posteriorly that was brought to the surface by the forelimbs. Second, *A. cisternasi* is a rapid, efficient forward burrower that is highly fossorial in habits. Conversely, *A. obstetricans* is a reluctant forward burrower that lingers on the surface and prefers to use pre-existing holes. Natural history notes also indicate *A. obstetricans* has a predilection for small mammal holes and crevices under stones or elsewhere (BOULENGER, 1896; DE WITTE, 1948; PASTEUR & BONS, 1959).

Of the two species under study, a greater osteo-myological specialization for burrowing is evident in the anterior portion of the body of *A. cisternasi* (forelimbs, hands, pectoral girdle, second-fourth presacral vertebrae, associated musculature; CRESPO, 1982b). This greater specialization is related to its adaptation to the warmer and drier Mediterranean environments which are typical of the southwestern Iberian Peninsula. These environments also show little variability, i.e., they are topographically more flat and open. Natural refuges are scarce, and the sandy soils are easy to dig into because they are quite friable. In contrast, *A. obstetricans* has a wider distribution covering areas with greater topographic relief. Many soil types are present and they are frequently firm. Thus, the soils often cannot be as easily penetrated by a burrowing anuran. An abundance of natural refuges occurs in these environments. Thus, the different burrowing behaviors and morphologies of the two species of *Alytes* are correlated with their environments.

Forward burrowing may have evolved in *Alytes* to assure subsurface concealment because of the involvement of the male's hind limbs in parental care. Observations indicate that the egg mass is not damaged by being covered with sand, nor by the thrusting movements of the hind limbs that are used to remove sand brought by the forelimbs to the surface. However, if the male were to burrow backwards, the egg mass might be loosened from the hind limbs, and the eggs could suffer abrasion/damage from the substrate. (The egg mass is covered with loose sand when forward burrowing is employed.) Furthermore, it would probably be difficult for a male to maneuver his hind limbs in such a manner to effectively dig a burrow large enough to accommodate the enlarged egg mass. A backward burrowing male would be apt to encounter difficulties negotiating around a buried object (e.g., stone) in his path. KROGH (1991), working in LEB's laboratory, compared the two species of *Alytes* with the backward burrowing *Bufo americanus* Holbrook, 1836 in regard to their ability to deal with buried obstacles (golf balls). *Bufo americanus* usually stopped burrowing when the obstacle was encountered. Some individuals tried to change direction, but they lacked the dexterity in their hind limbs to move around the obstacle. In contrast, *Alytes* simply burrowed forward in the direction that offered the least resistance, thereby successfully negotiating the buried golf balls. MUNSZ & TYLER (1977) suggested that buried root mats, stones, compressed rotten vegetation, and other impediments would block hind limb burrowers, and this was the probable selective pressure for the evolution of forward burrowing in the microhylid frogs they studied in Papua New Guinea. EMMERSON (1976) reported that headfirst burrowing by *Hemisus marmoratus* (Peters, 1854) was used for tunnel construction and that hind limb

burrowing is an inefficient mechanism for constructing horizontal tunnels. WAGER (1965) mentioned the construction of underground cavities for deposition of the egg mass by both *Hemisus guttatus* (Rapp, 1842) and *H. marmoratus*. Forward burrowing would be an advantage for such activities. The extensive tunneling as well as subterranean aggregative behavior by *Alytes* are also undoubtedly facilitated by forward burrowing. BROWN et al (1972) proposed that forward burrowing evolved in some anurans to facilitate subterranean feeding. Subsequently BROWN (1978) provided experimental evidence that the forelimb burrower *P. streckeri illinoensis* could feed underground. It is likely that the forward burrowing *Arenophryne rotunda* Tyler, 1976, *Hemisus marmoratus*, *Myobatrachus gouldii* (Gray, 1841), and *Rhinophrynus dorsalis* Duméril & Bibron, 1841 also feed underground because they consume mostly termites and/or ants (NOBLE, 1924, CALABY, 1956; PHILIPP, 1958, TYLER et al., 1980, TRUEB & GANS, 1983)

Backward burrowing frogs are largely inactive underground (EMERSON, 1976). Conversely, forward burrowing may be more common among frog species that are quite active underground (BROWN & MIANS, 1984). The coordination of sensory perceptions with motor patterns on the anterior end of the body could facilitate the most efficient forward progress. Furthermore, if the posterior end of the body is used for other purposes (e.g., parental care in *Alytes*), forward burrowing would be a necessity for concealment.

With all the advantages of forward burrowing, it is unusual that this behavior is not more commonly encountered, given the limitations of backward burrowing. However, the latter is predominant among the Anura, but rare in other tetrapod groups (HILLIUS, 1976). EMERSON (1976: 457) stated: "The large number of backwards burrowers in many anuran families may reflect a level of preadaptation for hindfeet digging in the morphological complex of saltatory locomotion." Furthermore, forward burrowing requires more extensive morphological modifications. HILLIUS (1976) suggested that backward burrowing was one of the main formative influences in the early evolution of the anurans. The body attains advantage by being concealed underground and is protected from dehydration. The head faces the opening and consequently the anuran can emerge quickly to pursue prey (HILLIUS, 1976).

Forward burrowing has independently evolved in several different anuran families. Thus, it is pertinent to compare this behavior among those species which have been most thoroughly studied. *Pseudacris streckeri illinoensis* (Hylidae) of the midwestern USA is a highly fossorial, rapid burrowing frog that makes exclusive use of its enlarged forelimbs (BROWN et al., 1972). Forelimb movements are synchronized in a stereotyped manner similar to a human swimmer doing the breaststroke. *Pseudacris ornata* of the southeastern USA uses the same motor patterns as *P. streckeri illinoensis* in forward burrowing (BROWN & MIANS, 1984). However, *P. ornata* is a reluctant forward burrower and uses its hind limbs to a limited extent for backward burrowing. Both species of *Pseudacris* vocalize underground, and construct tunnels or cavities in which push-up movements of the head stabilize the roof of the excavation (BROWN & MIANS, 1984, LFB, personal observations). Prior to burrowing, *Hemisus marmoratus* (Hemisotidae) of Africa probes the substrate in different areas with its snout to locate a suitable burrowing site (KAMINSKY et al., 1999). Forward burrowing involves up and down movements of the pig-like snout and alternate movements of the forelimbs (WAGER, 1965, EMERSON, 1976). The hind limbs either push the body forward or are not used in forward burrowing, and the species occasionally digs hind feet first into the substrate. *Arenophryne*

*rotunda* (Myobatrachidae) of Western Australia initially forces its head into the substrate and then utilizes scooping strokes of the forelimbs (TYLER et al., 1980). The hind limbs initially remain passive but later push the body deeper into the substrate. *Myobatrachus gouldii*, also a myobatrachid from Western Australia, burrows forward using the forelimbs with the assistance of the hind limbs (CALABY, 1956; PHILIPP, 1958). Detailed descriptions are lacking for the motor patterns of forward burrowing by the Papua New Guinea frogs (Microhylidae) studied by MENZIES & TYLER (1977). However, the anatomy of the skull and overlying integument suggest that the head plays a prominent role. *Rhinophrynus dorsalis* (Rhinophrynidae) of middle America is an accomplished backward burrower, and although behavioral observations are lacking, the extraordinary morphological specializations of the pectoral girdle and head leave little doubt that the animal is also a forward burrower (TRUIB & GANS, 1983). EMERSON (1976) briefly mentioned various other anurans in the families Bufonidae, Leptodactylidae, Microhylidae and Pipidae of Africa, Europe and South America that also apparently burrow forward or use their head for nest construction, but little information is available on their motor patterns. Thus, forward burrowing has independently evolved in at least nine anuran families on five continents for a variety of reasons. Although the motor patterns might appear superficially similar among the different species, there are differences in regard to synchronous or asynchronous use of the forelimbs, extent and nature of the use of the head, and degree to which the hind limbs assist the forward burrowing. Moreover, there are vast differences among the species in the structural specializations of the anterior portion of the body for forward burrowing (WAGER, 1965; BROWN et al., 1972; GALDIN, 1973; EMERSON, 1976; TYLER, 1976; MENZIES & TYLER, 1977; CRESPO, 1982a-h; TRUIB & GANS, 1983; BROWN & MEANS, 1984; TYLER et al., 1984; PAKSTIS & BROWN, 1987, 1991).

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